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Review

The plant Golgi apparatus—Going with the flow

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Abstract

The plant Golgi apparatus is composed of many separate stacks of cisternae which are often associated with the endoplasmic reticulum and which in many cell types are motile. In this review, we discuss the latest data on the molecular regulation of Golgi function. The concept of the Golgi as a distinct organelle is challenged and the possibility of a continuum between the endoplasmic reticulum and Golgi is proposed.

Keywords: Plant Golgi apparatus; Membrane flow; Protein trafficking

1. Introduction

Early electron microscopy (EM) studies revealed that plant cells contained organelles composed of closely apposed lamellae or cisternae, similar to the Golgi stacks described in mammalian cells [1,2]. This initiated decades of work on the biochemistry and the ultrastructure of the plant Golgi apparatus (GA). Since then, the unique aspects of the organisation and function of the plant GA has been regularly reviewed [3–6] and the differences in its organisation compared to other eukaryotes have often been discussed [6–8]. However, the unravelling of the genetic make up and molecular machineries of the plant secretory pathway has revealed significant homology with the mammalian and yeast counterparts [4–6,9]. Yet, despite this presence of highly conserved genes, the mechanisms by which the expression of these genes results in such phenotypic differences in both the structure and function of the plant GA has still to be unravelled. This also raises the question as to whether there is a basic set of rules that governs the operation of the secretory pathway across the kingdoms that can result in the varied levels of organisation reported to date. In this review, we consider some of the most recent observations on the organisation and dynamics of the plant Golgi apparatus and attempt to reconcile these with some of the earlier work on Golgi structure.

2. The plant Golgi apparatus: an organised profusion of membranes with adaptive specialisations

EM studies (structural, autoradiographical, immunocytochemical) have traditionally provided the basis on which the organisation and the function of the plant Golgi apparatus has been described [8,10,11]. More recently, the development of specific probes (antibodies, fluorescent protein-based Golgi markers) has permitted the visualisation of the Golgi apparatus by fluorescence microscopy [12,13]. It is now possible to carry out in vivo experiments on Golgi function and dynamics [9,14–17]. Moreover, imaging whole cells has permitted a better understanding of the structural and functional relations between the GA and its neighbouring membranous compartments, in particular between the ER and the GA [18–20].

As for other eukaryotic cells, the plant GA is a pivotal organelle in the secretory pathway, being a cross-roads in various trafficking events. Golgi compartments receive most

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of the ER-processed proteins, although export from the plant ER may by-pass the Golgi by a number of mechanisms. In the cereals and grasses ER, processed storage proteins may simply concentrate (oligomerise) and segregate within the ER lumen, and evolve into distinct storage compartments [21–23]. In cucurbits, so-called PAC vesicles (precursor accumulating vesicles) may carry protein cargo directly from ER to a storage vacuole [24].

Within the GA, ER-derived cargo molecules are further glycosylated, and the synthesis of complex polysaccharides characteristic of plants is undertaken. The plant Golgi is specialised in the synthesis and the export of complex glycans to the cell surface to organise the cell walls, which are mainly composed of polysaccharides (cellulose, hemicelluloses and pectins) [25,26]. Golgi-derived secretory vesicles carry these macromolecules to the plasma membrane [27,28]. Although synthesis of cellulose takes place on the plasma membrane, it also depends on the transport of membrane-bound enzymes, the cellulose synthases, from the Golgi to the plasma membrane. Certain glycosylation events are specific to the plant kingdom such as the addition of fucose and xylose to glycan chains [29–32] and recently a family of sugar transporters needed for complex polysaccharide synthesis has been described and located to the GA [33]. Lipid modifications are also important, many tasks taking place at the Golgi level, leading to a plant specific plasma membrane composition [34–36].

Mature cargo molecules (membrane or soluble) are differentially routed within the cell. Thus, another major function of the GA is the sorting and packaging of wall macromolecules and cargo proteins in membrane-bounded carriers to be targeted to their final destination. They may either reach the plasma membrane by exocytosis or other compartments of the endomembrane system, such as the vacuole, often via intermediate compartments such as the prevacuolar compartment (PVC). Here again, the processes are adapted to the cell type and the occurrence of a pleiomorphic and multifunctional vacuolar system is unique to plants [37,38].

Besides its pivotal role in secretion and vacuolar transport, the plant Golgi apparatus may also be involved in membrane recycling processes, either from plasma membrane [39,40], from the vacuolar system [41], or in the recycling of ER membrane [18,19].

A real challenge for the cell biologist is to understand how this transfer of cargo molecules is achieved within the endomembrane system. The development of cell-free assays, allowing the reconstitution of protein transport through the GA in mammalian systems resulted in the concept of trafficking by vesicular carriers [42,43]. It suggests that a membranous compartment (donor compartment) is able to provide a vesicle (carrier), which will fuse with another membranous compartment (acceptor compartment). In this concept, the compartments remain static. However, the early EM studies of Morre et al. describe the plant Golgi apparatus as a complex tubulo-saccular structure, with some contacts with endoplasmic reticulum [11,44–46]. Their observations raised the hypothesis of a membrane continuum within the endomembrane compartments. Finally, the description of the Golgi in some protists [47–51] has been the basis for the so-called cisternal maturation model. As cell wall scales were observed within the cisternal lumen, this model proposed that cisternae progressively move down the stack. These observations suggest that Golgi cisternae may evolve with time into different physiological or functional entities.

Whatever the nature of the cargo carriers in the Golgi stack, they appear to be associated with specific molecular machineries, and to be sensitive to the secretory inhibitor Brefeldin A (BFA). After BFA treatment Golgi markers have been reported to be either redistributed to the ER [13,19] or they accumulate within “BFA compartments” which by electron microscopy can comprise clusters of Golgi-derived vesicles [12,52,53]. In the former case, hybrid membrane structures composed of ER and Golgi have been reported in tobacco BY2 cells [54]. Such effects appear to depend on cell type and/or physiological conditions of the cells.

The occurrence of specific molecular machinery associated with endomembranes is now well established. Coat proteins (COPI, COPII, clathrin), small GTPases (Rabs, Arf, Sar1, Rac), fusion proteins (SNARES) and many others, appear well conserved throughout the eukaryotic kingdom, and their identification has in many instances paralleled the development of the vesicle carrier theory [55,56]. In plant cells, the majority of the COP I and COP II machinery and their associated effectors (respectively Arf and Sar1) has been cloned [57–60], although the exact role of the coat complexes in membrane and cargo transport has yet to be elucidated (see Section 3.2). Clathrin coated vesicles appear, as in mammalian cells, to be involved in the transport of hydrolytic enzymes from export sites at the trans-Golgi, to the vacuolar system ([43]; see Section 4.2). Regulation of the budding and fusion events between compartments is associated with the Rab [61–63] and SNARE [64,65] protein families, regulating specific steps of trafficking pathways, some of them being plant specific. Besides these protein families involved in membrane remodelling, some proteins have been identified as potential stabilisers for Golgi membranes, and described as “Golgi matrix proteins”. A few homologues can be found in the *Arabidopsis* genome, although a specific role in organisation of the Golgi has not yet been shown ([6,66], see Section 5). Finally, the families of motor proteins or their regulators, which should assure the transport of carriers between two compartments, are still poorly documented in plant cells [67–70].

Most of the data obtained by fluorescence microscopy have been interpreted taking into account the knowledge gained from earlier EM studies. However, in the latter case, a compartment has often be identified on morphological parameters meanwhile, in the former case, a compartment is identified by its ability to be recognised by specific markers.

It is interesting to consider the dynamics and organisation of the plant GA in the light of recent fluorescence studies, ignoring all the preconceptions from many years of electron microscopy. Ultrastructural evidence can then be mapped onto hypotheses generated from the recent immunocytochemical and live cell imaging studies.

3. The ER–GA complex

3.1. The ER–GA complex by light microscopy

The plant ER may be labelled with fluorescent dyes such as DiOC6 [71,72], by antibodies directed against soluble or membrane bound reticuloplasmins (i.e., proteins specifically identified as ER-resident such as calreticulin and calnexin) [73], against the ER-retention HDEL/KDEL sequences [74], or by specific GFP fusions [13,40]. In all cases, the ER appears as a membranous tubular network often mainly restricted to the cortex of mature cells and connected to the nuclear envelope. Although much talked about, with the exception of putative exit sites (see Section 3.2 below), from such studies, there is little evidence of specific sub-domains on the ER.

In contrast to the ER tubular network, staining of the plant GA reveals a punctate pattern composed of hundreds of distinct structures approximately 1 μm in diameter, as revealed using antibodies against peripheral glycoproteins [12,75]. Likewise, fluorescent protein fusions to a variety of proteins including the H/KDEL receptor, various mammalian and plant transferase signal anchor sequences, and sugar transporters, have all successfully located the plant GA [4,13,14,19,76,77].

All Golgi enzymes identified so far are integral membrane proteins. The mechanisms by which they remain specifically in Golgi appear to be related to the signal anchor sequence comprising the trans-membrane domain and flanking amino acids [78]. Interestingly, the signal anchor sequences from both rat and human transferases are sufficient for successfully targeting GFP to the plant Golgi indicating a consensus in mechanisms across kingdoms [13,19,79].

Labelling in living cells has shown that Golgi stacks are not static, but as well as moving in classic cytoplasmic streams, they also exhibit more specific movements. Individual Golgi stacks can move as fast as 2 μm per second [13,14], in an actin dependent fashion. Indeed, depolymerisation of actin induces the clumping of Golgi bodies within cells [80] and results in a cessation of movement [13]. It is assumed that the motor driving the Golgi is myosin. However, a Golgi-associated kinesin has also been identified in cotton and arabidopsis (GhKinesin13a and AtKinesin-13A) [81,82] and Golgi bodies were also shown in association with microtubules. It was suggested that microtubules may also be involved in the organisation of Golgi bodies at the cell cortex, although the authors concluded that kinesin-13A does not in fact contribute to the primary movement of the Golgi.

Co-visualisation of ER and the GA suggests that Golgi bodies are associated with the cortical ER network. When fused to GFP and expressed in tobacco leaf epidermal cells, the arabidopsis homologue of the H/KDEL receptor AtERD2 is localised both in the ER membranes and Golgi membranes [13,18,19]. Golgi bodies appear attached to the ER membranes and appear to move over the surface of the ER tubules. This close association can also be seen with dual expression of an ER construct such as signal peptide-GFP-HDEL and ST-mRFP (Fig. 1). Preliminary studies using optical tweezers in an attempt to separate fluorescent Golgi bodies from ER confirm the strong attachment of Golgi membranes to the ER (Leru and Brown, unpublished data). The fact that biochemical separation between ER and Golgi membranes is difficult in plant cells further confirms the tight association between ER and GA. These features indicate a possible membrane continuum between ER and Golgi. Most of these live cell imaging studies have been performed on the current models used in plant cell bioimaging, mostly BY-2 cells, tobacco and arabidopsis leaves. The relation between ER and Golgi may, however, differs according cell specialization and should be further investigated in other tissues.

The structural and functional link between the ER and GA and the kinetics of transfer of membrane cargo molecules between ER and GA have been investigated using fluorescence recovery after photobleaching (FRAP) techniques. FRAP of Golgi targeted GFP constructs in tobacco leaves has shown that transfer of cargo molecules from the ER to Golgi is energy dependent, but not dependent on the cytoskeleton. Such transport can occur

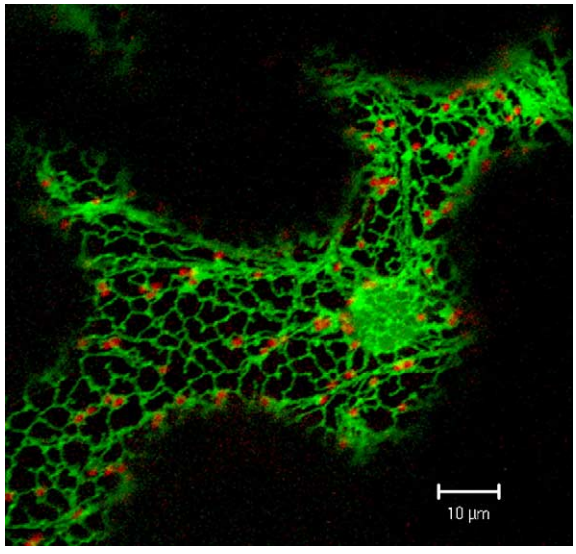

Fig. 1. Dual expression of a signal peptide-GFP-HDEL construct and a rat sialyl transferase signal anchor sequence-RFP in an epidermal cell of a tobacco leaf. Note the close association of the Golgi bodies with the ER network. Micrograph courtesy of John Runions, Oxford Brookes University. Bar=10 μm.

when the Golgi stacks are static and also when they are moving [18,20]. These data supported the hypothesis that there may be some form of structural continuity between the two organelles permitting direct transfer of cargo without the requirement for vesicle vectors. It also questions the mechanisms of putative retrograde transport by vesicle carriers.

3.2. The ER–GA complex associated machinery

If there are in some instances direct connections between the plant ER and Golgi bodies, even if they are transitory, can this be reconciled with the presence of specific molecular machinery? Presumably, a microdomain in the ER membrane has to become competent either for producing a profusion of membrane, which either evolves into GA membranes, or is capable of fusing to or bridging to the existing Golgi membrane. It is therefore not unreasonable to expect that specific molecular machinery will accumulate at the sites where Golgi stacks are attached to the ER.

3.2.1. The COPII machinery

It has been suggested that COPII coats may be necessary for ER to Golgi transport processes in plant cells [60,83–86]. Recent data suggest that Sar1p, the activating GTPase for COPII coat recruitment could play an essential role in the formation of ER microdomains associated with Golgi membranes. In the presence of Golgi targeted GFP constructs Sar1p defines punctate structures on the ER membranes, as does the GTP-locked mutant of the protein at low levels of expression [20]. The requirement of Sar1p for export out of the ER has been demonstrated in vivo by inhibition of secretion after the expression of non-functional mutant forms of the protein [20,83,87]. Double expression of fluorescent protein Sar1p and Golgi constructs showed them to apparently co-localise on the ER membrane and to move together as a unit along the ER membrane. Because of this, the concept of a motile secretory complex consisting of Golgi and ER exit sited was proposed [20]. Over expression of both GTP and GDP locked mutants of Sar1p resulted in a redistribution of Golgi markers to the ER, resulting in a phenotype similar to that observed after BFA treatment [20,83,87].

Biochemical studies have shown that Sar1P mediates the recruitment of two major protein complex (sec13/31p and Sec23/24p), building up the typical COPII structures described in mammalian cells [60]. In plant cells, no functional studies of these proteins have been described, nor the binding of COPII to specific motifs of Golgi resident proteins. A recent report suggests that a cytoplasmic dibasic motif within Sar1p may function as a receptor for Golgi resident enzymes in mammalian cells [88]. Thus, the occurrence of specific bonds between GA proteins and Sar1p may contribute to the differentiation of specific ER microdomains competent for producing Golgi membranes.

The GTPase activity of Sar1p is regulated by an exchange factor, Sec12p, which in tobacco leaf epidermal cells has been shown to be uniformly distributed over the ER network. Therefore, it should not play a role in the differentiation of ER membranes into Golgi. This distribution of Sec12 is similar to that in *Saccharomyces cerevisiae* where the Golgi exists as dispersed individual cisternae [8,89]. However, in *Pichia pastoris*, which has static Golgi stacks, Sec12p is restricted to the ER export sites [89]. Perhaps, the distribution of Sec12 is dependent on the relative mobility of the Golgi and the export sites feeding them.

In mammalian and yeast cells, it has been proposed that COP II components act in a highly regulated manner to recruit some specific ER membrane areas in coated vesicles, which in turn would transport these membranes and their associated cargo molecules to an intermediate compartment forming discreet transport vesicles [90]. As can be seen from the recent work described above, this concept may very well not be applicable to plant cells. Data strongly suggest that COPII components may indeed be needed for some cargo accumulation and for regulating export out of the ER [59]. However, there is, to date, no experimental argument to suggest that COPII vesicles exist or are the carriers for cargo export between the ER and GA. The fact that in many plant cells, this ER/GA step is cytoskeleton independent is a further argument against the involvement of a specific vesicle carrier between the two compartments [18,19]. Interestingly, it has also been shown that in plants, transport from ER to GA can also be COPII independent [91]. The concept of the biogenesis of COPII independent carriers from ER export sites is also becoming fashionable in mammalian cells [92,93].

3.2.2. The COPI machinery

Homologues of the proteins of the COPI coatomer complex in plants have been cloned [57,58,60,94]. Immunofluorescence studies have shown the proteins located to the Golgi with no evidence of any location on the ER, and they may react differently to BFA according the plant material studied [54,95,96]. COPI components seem to interact in vitro with the di-lysine motifs of specific ER membrane proteins [94]. In the animal kingdom, COPI is thought to be involved in retrograde transport from GA to the ER although there are little data which confirm this directionality in plant cells.

Interestingly, the location of Arf1P, the COPI-associated GTPase, does not seem to be restricted to the GA. GFP constructs have shown ARF1 to be located at the Golgi [97], but immunofluorescence has also shown that the protein may be located on the ER, and the plasma membrane [95], suggesting that it may function at different levels of the secretory pathway. It may very well have multiple roles in that it functions in the trafficking of the H^+ ATPase from the GA to the plasma membrane, in the positioning of sialyltransferase to the Golgi, in the maintenance of the

endoplasmic reticulum [98,99], and with the regulation of vacuolar secretion [97,100]. Thus, there is increasing evidence that ARF1 acts at multiple sites in the cell and may participate in membrane remodelling with distinct mechanisms apart from its COPI recruitment function. Such specific ARF1 activities may be regulated by the specificity of effector molecules such as ARF GEFs (guanine nucleotide exchange factors [96,101], or ARF-GAPs (GTPase-activating proteins, [102]).

The question remains as to whether ARF or COPI play a role in regulation of the ER/Golgi complex? Although there are, to date, little functional data to suggest COPI coat involvement in ER/GA cargo exchanges, BFA has been shown to affect fluorescence recovery of bleached Golgi–GFP constructs [18]. Also, a GTP-locked (Q71L) mutant of Arf1 has been shown to inhibit the targeting of sporamin–GFP to the vacuole in arabidopsis protoplasts, resulting in a build up of fluorescence in the ER [97]. These data suggest that in plant cells Arf1p may play a major role in the construction of ER export sites and in Golgi biogenesis from export sites, as has been proposed for mammalian cells [103].

The exact functions of COPI and COPII complexes, as in animals, still have to be elucidated in plant cells. Their ability either to form coated vesicles or to define specific recruitment domains within ER and GA membranes may be necessary for modelling the membrane dynamics (creation of microdomains) and maintaining the identity of each membrane [95]. This may require such a total interdependence of the COPII and COPI pathways for the recycling of regulatory machinery such as the SNARE fusion molecules, that disruption of either route will result in the collapse of the other [6].

3.2.3. Regulatory machinery at the ER/Golgi interface

No matter what the exact structural nature of the ER/Golgi interface is in plant cells, it is becoming clear that other proteins shown to be involved in this transport step in mammals and yeasts most likely operate in plants as well. Recently, from an analysis of the NCBI protein database, out of 54 SNARES in the arabidopsis genome, 15 SNARE molecules have been identified as being located to the ER and Golgi apparatus [104]. Of these, 6 were ER localised. Thus, there are a number of SNARES potentially involved in ER to Golgi transport, and their exact function are currently under investigation.

Similarly, functional studies on plant Rab proteins are still in their infancy. At least one Rab protein has been shown to regulate ER to Golgi transport in plants. A dominant inhibitory mutant of the arabidopsis homologue of Rab1 (AtRabD2a previously AtRab1b) [62,63] has been shown to affect transport of a secretory version of GFP out of the ER in tobacco leaf epidermal cells [105]. This effect was rescued by co-expression of the wild type protein but not by other Rabs. The same construct also slowed down the reformation of Golgi stacks in tobacco leaves after BFA induced redistribution of Golgi membrane into the ER [19]. Likewise, it has also been suggested that an arabidopsis homologue of Rab2 (NtRabB2) may regulate transport of cargo between the ER and Golgi in pollen tubes [106]. The likely locations of these plant Golgi associated proteins are summarised in Fig. 2.

3.3. The ER/GA complex at the ultrastructural level

Electron microscopy of higher plant cells has not revealed the geometrical organisation of the cortical

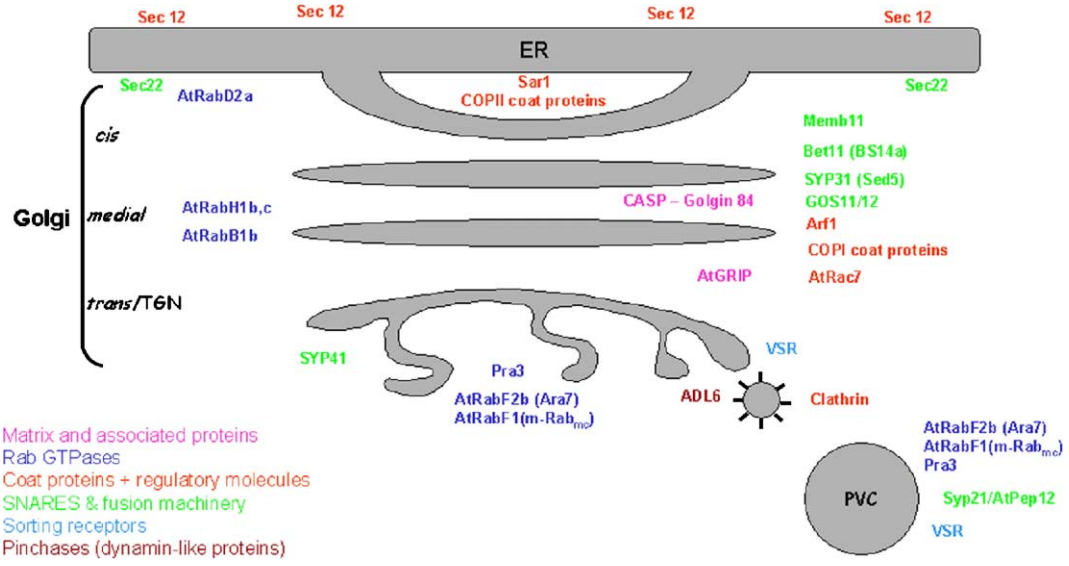

Fig. 2. The likely location of some of the Golgi associated proteins identified to date in plant cells. The trans-Golgi and trans-Golgi network are represented as one cisternum although it is likely that the TGN may in cases slough off from the Golgi stack. The exact location of many of the proteins within the Golgi stack such as CASP, Golgin 84, AtGRIP and some of the SNAREs has yet to be determined.

network of ER tubules as seen after in vivo staining with fluorescent dyes or GFP expression. Although the cortical distribution of ER in cells has been reported many times [107,108], specific ER exit sites associated or not with coated vesicles have not yet been reported from either thin section or freeze-fracture EM. Similarly, the structural association between ER and Golgi is not immediately obvious from conventional electron micrographs. In contrast to what has been described from in vivo imaging with Golgi targeted GFP constructs, when observed in ultra-thin sections, Golgi stacks may appear to be remote from ER membranes. However, observations on thick sections have revealed the presence of interconnections between ER tubules and the tubular periphery of the Golgi stacks [8,109,110]. Moreover, ER membranes and *cis*-Golgi membranes show similar reactivity to cytochemical agents, suggesting a close biochemical relationship [8].

The polar organisation of the GA has been determined from ultrastructural studies and has often been correlated with a functional subdivision of the stack into cis-medial and trans-cisternae. According to the concept of membrane flow described by Mollenhaueur and Morré [11], the cis face would correspond to the entry site/forming face of the Golgi, and the trans-face to the exit/maturing site. This subdivision does not correspond however to a strict compartmentation of Golgi markers. The products of Golgi enzymes have been shown to be distributed in a differential manner over the plant Golgi stack [29,30,111], and they may correspond to microdomains linked to progressive metabolic events rather than a strict compartmentation. Likewise, storage proteins, such as legumin and vicilin in developing pea cotyledons, have been shown to mature and be segregated into vesicles as far back as the cis-face whilst other proteins can be inserted into the same vesicles as they migrate towards the trans-face [112,113]. Negative staining of isolated plant Golgi stacks showed the occurrence of many interconnections between the cisternae as well as tubules forming networks at the periphery of the cisternae [114]. In thin and thick sections of tissue in which endomembranes were stained selectively with osmium tetroxide/zinc iodide the appearance of membranous tubules forming a continuous network within the Golgi stack has also been reported by several authors ([4,8,109, 115] see also Fig. 3).

In summary, in vivo imaging suggests an ER/Golgi continuum and some EM data supports this hypothesis. However, to date, ultrastructural studies have often been based on slow chemical fixation and cytochemical reactions, which may induce structural artefacts, although most of the basic features of the Golgi stack have been confirmed by the application of ultra-rapid freezing techniques [4,116]. It will probably require a combination of freezing technology, freeze-substitution and EM tomography to reveal the true structure of the plant Golgi stack and the ER/Golgi interface at relatively high resolution and we can expect this to vary between cell types with different cargo export programmes.

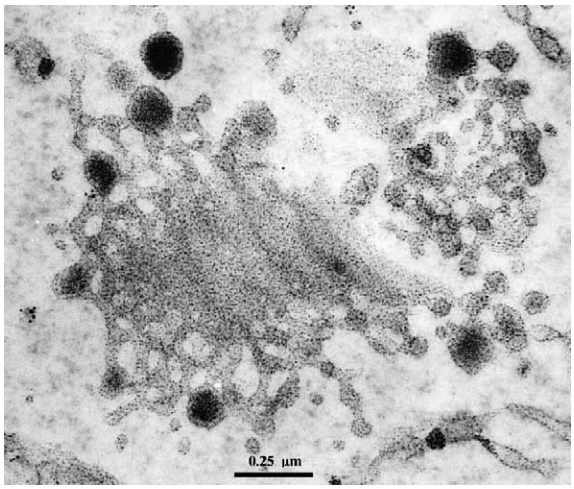

Fig. 3. Golgi stack in tangential view in maize root cell (reduced osmium/silver proteinate staining, outlining the carbohydrates). Periphery of the Golgi stacks is organised in tubular areas and connective links between cisternae can be seen. Secretion products segregating at the tubular periphery of the Golgi are intensively stained.

4. The Golgi stack and post-Golgi complex

The conventional scheme of plant trafficking pathways suggests that cargo molecules on exit from Golgi stacks, are transported either to the cell surface (exocytosis) or to the vacuolar compartments (vacuolar secretory pathways). The major questions to be answered are at which structural level do Golgi membranes acquire the ability to differentiate between these pathways and what is the level of involvement of post-Golgi intermediate compartments in this part of the secretory pathway?

The current picture for trafficking events downstream of the Golgi is complex and somewhat confusing. The identification of post-Golgi compartments by fluorescence microscopy has been hindered due to a dearth of specific markers for such organelles. Except for one attempt [117], they have also never been biochemically isolated, and thus their definition remains quite empirical. In the last few years, a number of molecular markers for the trans-Golgi and post-Golgi compartments have been identified, including SNARES, Rabs and sorting receptors [61,104,118–120], but the ultrastructural location of many of these proteins has yet to be confirmed. The complexity is reinforced by the fact that several vacuoles exist in plant cells, suggesting different vacuolar pathways, which in some cases may even overlap [37,38]. As in mammalian cells, it is most likely that there is a confluence of the endocytic and secretory/vacuolar pathway downstream of the Golgi apparatus [40,41].

4.1. From GA to the plasma membrane: a default pathway?

Leaving the Golgi stack for the plasma membrane is one option for secretory molecules. All fluorescence labelling experiments suggest a direct rapid and specific transfer to the plasma membrane as no specific intermediate compartments between the GA and plasma membrane are labelled by the secretory products either newly synthesised or processed in the GA [52,105,121,122]. This difficulty in imaging secretory products in transit is most likely related to either a low level of product, or to the speed of transport through the system. To further reinforce this hypothesis, blocking secretion by brefeldin A often causes an accumulation of the secretory products, either within the cytoplasm into post-Golgi "BFA compartments" [52,121], or within the ER [105,122,123].

Data on the recycling of membrane proteins suggest that the BFA compartments may represent an amplification of a pre-existing compartment, or may be formed de novo from Golgi or plasma membrane (see discussion in [6,41]). Whether this compartment is an intermediate along the secretory pathway, which also has a recycling function, has still to be clarified.

As it stands, these data provided by light microscopy suggest that exit from the GA to the plasma membrane occurs by bulk flow, without other checkpoints on the way to the cell periphery. The transport of polysaccharide molecules from GA to the plasma membrane may be easily mapped by EM either by specific cytochemical staining [124] or by immunolocation of Golgi-derived products [125,126]. This transport from GA to cell surface is mediated by secretory vesicles of varying size which can carry mixed cargos of polysaccharides [125] or polysaccharides and glycoproteins [126]. The secretory vesicles may be considered as the final processing compartment for cargo maturation as esterification of pectins or further polymerisation of polysaccharides may occur within the vesicles during transport to the plasma membrane (Vian B., personal communication). To date, no protein coats have been found associated with such secretory vesicle. Their maturation can be associated with different Golgi cisternae [8], and electron microscopy suggests that they may detach at different levels down the Golgi stack [126]. Biochemical studies suggested that targeting of GA-derived soluble cargo products is by default. No positive signals have been found associated with the transport of ER/GA-derived secretory products to the plasma membrane [127].

The situation with membrane proteins has, however, been controversial, as both the tonoplast and the plasma membrane have been considered as the default pathway for membrane proteins [128,129]. Certainly, the transmembrane domain (TMD) of single pass membrane proteins is capable of directing chimeric proteins to different membranes. GFP constructs made with the membrane-spanning domain of the human lysosomal protein LAMP1 are directed to the plasma membrane. However, deletions in the TMD resulting in 20 or 17 amino acids resulted in the constructs being resident in the Golgi and ER, respectively [130]. Likewise, when the TMD of a protein usually targeted to the vacuolar pathway (the vacuolar sorting receptor BP80) was increased to 22 amino acids the GFP reporter was transported to the plasma membrane. However, at least for polytopic proteins like plasma membrane H^+ ATPases, it has been recently proposed that one or more signals may be required for sorting through the exocytic pathway [122].

In all cases, involvement of molecular equipment such as coat complex, adaptors or receptors have never been reported to be associated with polysaccharide or glycoprotein sorting to the plasma membrane. Arf1p and COPI antibodies have shown in certain cases a staining of both Golgi and plasma membrane [95]. However, this dual location may reflect recycling by COPI vesicles between the new plasma membrane being formed (made of Golgi-derived membranes) and the Golgi stacks [95]. A total of 18 different SNARE proteins have been located to the plasma membrane [104] which have the potential for conferring some level of specificity on vesicle fusion. However, it has also been suggested that some of these proteins may also act in a signalling capacity which may explain the high number of plasma membrane SNARES [131].

The possibility of differential targeting within the exocytotic pathway has arisen from studies on proteins associated with auxin efflux (PIN proteins) which have a polar distribution in the basal plasma membrane of *Arabidopsis* root cells [101,132]. However, this hypothesis has still to be proven and preliminary studies strongly suggest that the insertion of PIN proteins within membranes may first occur in a non-polar fashion, and that polarity would be the result of post-deposition organisation of the proteins within the plasma membrane. (Boutte and Satiat-Jeunemaitre, unpublished data). However, one specific event in the cell cycle, that of cytokinesis, involves very directed trafficking of Golgi-derived secretory vesicles. The SNARE SYP111 (KNOLLE) is also specifically expressed during mitosis and is found only on the developing cell plate [133–136].

Another way to regulate the transport of Golgi-derived membranes would be through the cytoskeleton, as exocytosis of Golgi-derived vesicles is likely to be actin mediated [67,68]. Interestingly, over-expression of one GFP-conjugated Rac protein AtRac7, which targets actin cytoskeleton via actin depolymerising factor, but not other GFP-tagged Rac proteins, induces a labelling both at the Golgi and at the cell surface in pollen tubes [70].

4.2. From GA to vacuole

In contrast to the bulk flow hypothesis of transport to the plasma membrane, trafficking to the vacuole relies on the recognition of specific vacuolar sorting motifs. It is now generally accepted that there are two major routes of secretion from the Golgi to the vacuolar system [37,137,138]. Firstly, a

direct transport of protein to the storage vacuole via dense vesicles such as described in developing pea cotyledons [112,113,139]. Little is known about the mode of trafficking and targeting of these vesicles to the correct compartment, although sorting relies on a carboxy-terminal propeptide and may be receptor mediated as transport to the storage vacuole is saturable [140]. These dense vesicles may form as early as the cis-face, however, it is assumed that they depart the Golgi only towards the trans-face ([113], see Section 3.3).

Secondly, transport of protein to the lytic vacuole is mediated by a family of vacuolar sorting receptors (VSR) resident in the trans-Golgi or trans-Golgi network (TGN), and they are carried in clathrin-coated vesicles to a prevacuolar compartment (PVC). VSRs are related to the receptor BP80 (VSRps-1) first cloned from peas [141,142]. Homologues to this protein have now been identified in various species [143]. VSRs are integral membrane proteins which can bind clathrin through adaptin-binding tyrosine motifs in their cytosolic tails [142]. They recognise sequence-specific NPIR (vacuolar) motifs that may be present on either termini or internally in the cargo protein and cycle between the Golgi and the PVC [38,144–146]. These VSRs also co-localise with the SNARE PEP12(At-SYP21) which belongs to the syntaxin family which has been localised on structures distinct from GA and termed the PVC [64,117–119,147–149]. Specific Rab proteins such as AtRabF2b (ARA7) and homologues of Ara6 have also been located to the PVC [61,120,149]. These various markers for PVC are BFA insensitive, and by fluorescence microscopy reside mainly on a compartment distinct from Golgi and vacuole. They may, however, exhibit a low amount of colocalisation with the Golgi (10–20%), suggesting that they are involved in the recycling of VSRs from PVC to the GA.

This relatively simple concept of separate sorting pathways for storage and lytic proteins is challenged by a recent study, which suggests that the situation may not be so straightforward. In developing castor bean seeds, the VSR apparently binds the proteins, proricin and pro2S albumin, which are destined for the storage vacuole [152], suggesting that clathrin-coated vesicles may also carry these proteins. Likewise in arabidopsis seeds, a knock out of AtVSR1 has been shown to result in the partial secretion of precursors of major classes of storage proteins [153].

A recent EM study on high-pressure frozen freeze-substituted tobacco BY2 cells has shown that VSR antibodies label putative endocytic compartments, the multivesicular bodies (MVBs), which may also function as PVCs [117]. MVBs in plants are compartments, which were first functionally defined at the EM level, as organelles on the endocytic pathway, as they accumulated endocytosed cationised ferritin [39,150,151]. These data suggest that PVC may in fact function in both the endocytic and vacuolar pathways. In all cases, both storage and lytic pathways and their associated sorting events require the presence of a trans-Golgi sorting compartment. Thus, the trans-Golgi or TGN may in the appropriate tissue be able to sort both lytic and storage cargo.

Scission of cargo laden clathrin coated vesicles at the trans-Golgi is most likely mediated by dynamin-like proteins. An *Arabidopsis* dynamin-like 6 (ADL6) has been shown to be located at the trans-Golgi and a dominant negative mutant caused accumulation of lytic vacuole cargo at the Golgi but had no affect on the transport of plasma membrane bound cargo [154].

4.3. What is the trans-Golgi Network?

The exact nature or even the presence of a functionally distinct TGN in plants is a matter of considerable debate. This has been made all the more confusing due to data emerging on the location of various marker molecules, from both immunofluorescence and fluorescent protein expression, which have yet to be reconciled with existing ultrastructural data. The trans-most face of the Golgi stack can exhibit various structural profiles. Some stacks may have an obvious final cisternum which is cohesive with the rest of the stack but which may exhibit varying degrees of tubulation [8,116]. However, in other cases, the trans-most cisternum may appear to be partially detached from the Golgi and ultimately, a cisternum-like structure may appear fully distinct from the Golgi stack and have a tubular/vesicular profile [155]. In most cases, clathrin-coated vesicles are associated with this last cisternum or network. These variations are probably the result of a highly dynamic process in the Golgi membrane transformation. The term trans-Golgi network TGN has often been ascribed to all of these manifestations of the final cisternum in the stack. A number of SNARE proteins have been located to the trans-most cisternum by gold labelling including SYP41, SYP61 AtVTI12 and AtVPS45 [119], which these authors termed the TGN. The trans-Golgi cisternum or TGN bears a remarkable similarity to the partially coated reticulum, first described as a tubulo-vesicular compartment, with clathrin buds, which can rapidly accept internalised ferritin in protoplasts [39,150,151,156,157]. Thus, it has been suggested that this compartment may function as an early endosome, even if it may in some cases be structurally continuous with the TGN [155].

By light microscopy, it is hard to define a structurally distinct TGN. However, from an analysis of the arabidopsis SNARES, it was demonstrated that a fluorescent protein constructs of SYP41 and SYP61 co-located and were sometimes in close proximity to the Golgi apparatus but most often was located to punctate structures separate from the Golgi [104]. On BFA treatment, these structures clumped but unlike many of the Golgi SNARES showed no ER location. From this analysis, it was concluded that SYP41 and 61 located to the TGN. Of the other SNARE constructs analysed, AtVTI11/13 located to the TGN and the vacuolar membrane and AtVTI12 located to the TGN

and PM. AtVTI11/12/13 also sometimes colocated with a PVC marker SNARE SYP22. It is a possibility that these data indicate that the TGN forms from the trans-Golgi and sloughs off into the cytosol as a functionally distinct entity. It will be interesting to find out if the SYP41/61 compartment is in fact the same structure as the so-called partially coated reticulum first described in the 1980s [151,157]. This leaves open the question of whether trafficking from the Golgi to the prevacuolar compartment can take place from the trans-most Golgi cisternum, a TGN attached to the Golgi stack, a functionally separate TGN or all three.

5. Golgi dynamics and biogenesis

5.1. Golgi membranes emerge from ER domains

The recent bio-imaging studies of the plant Golgi favour the theory of a continuum between the ER and GA. This continuum may also operate through the whole Golgi stack, and from early EM studies such membrane connectivity has been postulated for Golgi and post-Golgi compartments. However, the Golgi stack is a functionally distinct compartment, identified with specific markers. This apparent paradox may find an explanation in the mechanisms of Golgi dynamics and biogenesis.

The extremely close association of the Golgi and the ER in the live cell imaging systems makes it tempting to speculate that the Golgi may be considered as a differentiated domain of the ER. Thus, regulation of Golgi number in a cell would depend specifically on the control of membrane flow out of the ER exit site. In favour of this hypothesis, come the studies performed on living tissues such as leaves and suspension culture cells, where Golgi stacks can reform after BFA-induced re-absorption of Golgi membranes into the ER and such reformation can take place in the absence of any cytoskeleton and in the absence of protein synthesis [19]. Golgi biogenesis from the ER membrane has also been suggested in other eukaryotic cells. In most of the cases, the ER-GA transition has been described via the formation of tubular and fenestrated structures (see [8] for references). In the yeast *Pichia pastoris* de novo formation of Golgi stacks can occur from the ER [158]. Likewise, in mammalian cells, in the absence of microtubules, the formation of fluorescent Golgi mini stacks positioned next to ER exit sites has been reported in cells expressing a galactosyl transferase-GFP construct [159]. Therefore, the differences in Golgi organisation between kingdoms would be marked by its ability to organise these ER-produced membranes rather than in their biogenesis. The plant GA appears as an intermediate stage in terms of evolution strategy, as most yeasts are producing single Golgi cisternae, plants are characterised by cisternae organised in Golgi stacks and animals in most cases exhibit gatherings of Golgi stacks organised as a perinuclear ribbon. In all cases, the acquisition of molecular signature of the Golgi has to be explained. All along the secretory pathway, it is well accepted that there is a progressive transformation of lipids within the membrane paralleled with a progressive transformation and accumulation of secretory products within the lumen (Fig. 4). Finally, several physico-chemical gradients are established within the endomembrane system (pH, lipid species, protein content of membranes). These membrane differentiation events and established gradients may help explain the distinct molecular signature of ER and Golgi.

5.2. Building a Golgi stack

As discussed earlier, data from the expression of Golgi targeted fluorescent protein constructs reveal them to be highly motile over the surface of the ER, moving at up to 2 μm a second and even faster when caught in a cytoplasmic stream. The question then arises as how the stacks of cisternae manage to maintain their integrity and not literally be torn apart by shear forces as they move through the cytosol. It is possible that there is more membrane interconnection between cisternae than had been previously thought and depicted in various models. It has also been suggested that the whole Golgi stack is surrounded by a ribosome excluding matrix, which may bind the complete structure together [155], although no proteins from such a matrix have been characterised. The well-documented intercisternal elements, which are more prevalent towards the trans-face, may also be involved in binding cisternae together [54,116,160]. It is also possible that oligomerisation of transferases could stabilise the cisternae. Although it is not easy to reconcile this with the rapid turnover of membrane proteins as shown by FRAP technology [18], it has been shown that aggregation of a medial N-acetylglucosaminyl transferase does not stop it travelling to the trans-Golgi at the same rate as a cargo protein [161].

In mammalian and yeast cells, many so-called Golgi matrix proteins have been characterised which may have varied functions from the tethering of percolating vesicles, through to interactions with the cytoskeleton and regulatory Rab proteins [162–165]. In plants, homologues of some of these proteins are starting to be reported. For instance, a GRIP domain protein has been identified in arabidopsis and fluorescent protein fusions with the C-terminal domain co-located to the Golgi with a α-mannosidase construct indicating Golgi location [66]. Likewise, from the construction of a database of coiled-coil proteins in arabidopsis, three proteins homologous to CASP and golgin-84 were identified [166]. Undoubtedly, database mining will reveal more homologues of the Golgi associated proteins which in turn will reveal various binding partners. Perhaps, the next major advance in our understanding of the development and maintenance of the plant Golgi stack will come from data on the function of the matrix proteins.

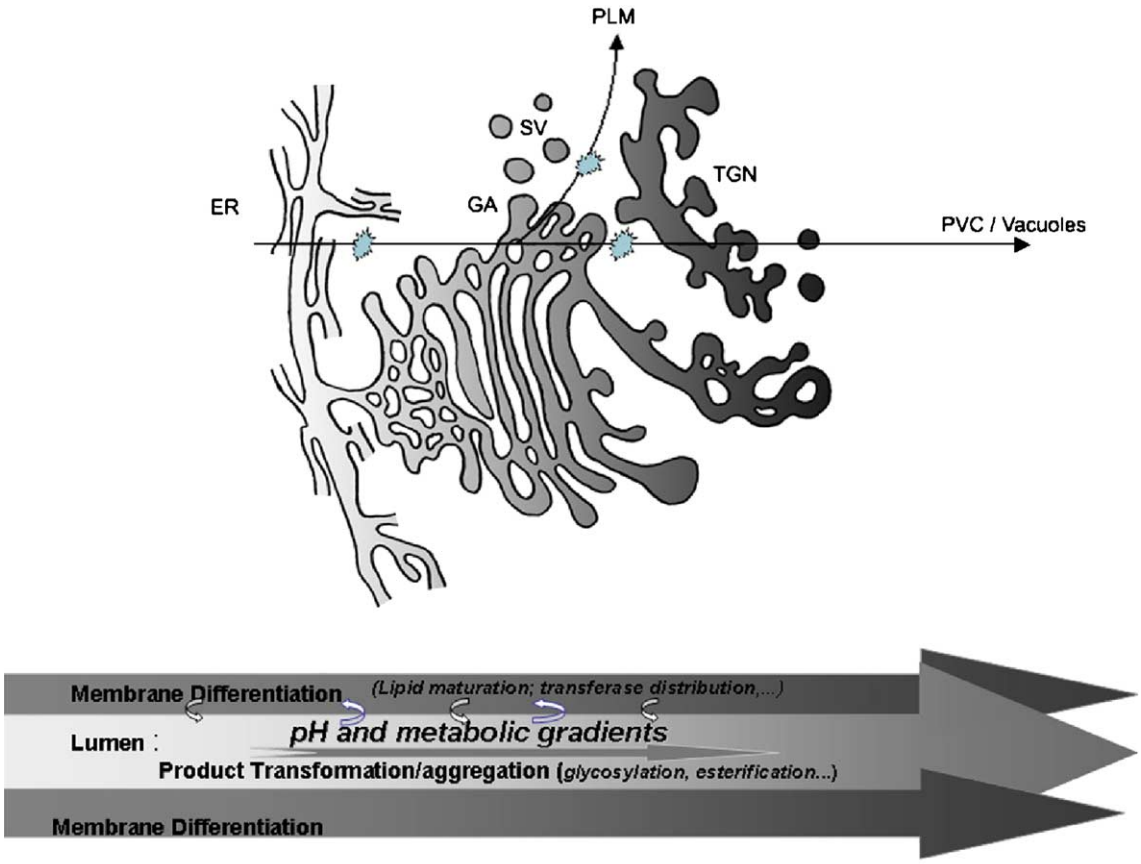

Fig. 4. The Golgi stack going with the flow: the endomembrane system seen as a progressive differentiation of membrane from ER. Top: the Golgi stack may be considered as a differentiation of ER membranes, acquiring molecular identities via the evolution of the different gradients. The ER/GA connection may be transient, or permanent according the cell system. Rupture/scission events occur along the membrane continuum, leading to a structurally distinct Golgi compartment with new physico-chemical properties, a structurally separate trans-Golgi network and secretory vesicles. Bottom: progressive differentiation of membranes is paralleled with progressive changes within the lumen, and constant interactions between the two may provide positional informations within the gradients.

5.3. Is the Golgi stack an organelle in its own right?

The concept of the Golgi stack as an ER-linked ephemeral organelle, as discussed previously, questions the existence of the Golgi as a distinct morphological organelle in its own right. However, there are plant tissues, such as root cap statocytes, where the Golgi stacks appear remote from the ER. Although no data from live cell imaging of such cell types are available to date, they suggest that scission events between the Golgi and the ER take place at some earlier stage in the maturation of the endomembrane system (Fig. 4) perhaps within the meristem before cell type differentiation. However, the fact that Golgi biogenesis, through the extrusion and differentiation of ER-derived membrane, has yet to be described at the EM level, suggests that this may be a rapid process. The occurrence of the separation of the two organelles along the membrane continuum would lead to the rupture of the established gradients and would contribute to the creation of a structurally distinct and independent Golgi compartment with its own physico-chemical properties. It can be considered that separation events similar to an ER/Golgi scission may also take place between the tubular extensions described at the trans-face of the Golgi, leading to the formation of the TGN and perhaps the prevacuolar compartment.

6. Conclusion

It is apparent that most of the molecular machinery associated with transport events is present in plant cells as in any eukaryotic cell (Fig. 2). However, it is becoming clear that the expression and localisation of the particular genes is not necessarily sufficient to explain the mechanics of the secretory pathway or the differences in the pathway between kingdoms. They still may point to some basic rules for a progressive differentiation of membranes from ER to GA and through the GA and to the post-GA compartments. Moreover, it is also becoming clear that the concept of organelles along the secretory pathway being discreet entities fed by shuttles of anterograde and retrograde vesicles may not be an accurate reflection of the dynamics inside a cell. Evidence from live cell imaging and recent develop-

ments in electron microscopy, such as tomography, are suggesting that we have to consider that there may be a membrane continuum between the various membrane-bounded compartments of the secretory pathway (Fig. 4) [6,8,93,167]. Therefore, the endomembrane system (including the Golgi apparatus) appears as a dynamic entity in equilibrium, maturing along the secretory gradient from the ER to the PM or vacuolar system.

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References

[1] A.J. Dalton, M.D. Felix, Cytological and cytochemical characteristics of the Golgi substance of epithelial cells of the epididymis-in situ, in homogenates and after isolation, Am. J. Anat. 94 (1954) 171–208.
[2] D.G. Whaley, M. Dauwalder, The Golgi apparatus, the plasma membrane, and functional integration, Int. Rev. Cytol. 58 (1979) 199–245.
[3] P. Dupree, D.J. Sherrier, The plant Golgi apparatus, Biochim. Biophys. Acta 1404 (1998) 259–270.
[4] U. Neumann, F. Brandizzi, C. Hawes, Protein transport in plant cells: in and out of the Golgi, Ann. Bot. 92 (2003) 167–180.
[5] G. Jürgens, Membrane trafficking in plants, Ann. Rev. Cell Dev. Biol. 20 (2004) 481–504.
[6] C. Hawes, Cell biology of the plant Golgi apparatus, New Phytol. 165 (2005) 29–44.
[7] M. Pavelka, D.G. Robinson, The Golgi apparatus in mammalian and higher plant cells: a comparison, in: D.G. Robinson (Ed.), The Golgi Apparatus and the Plant Secretory Pathway, Blackwell, Oxford, UK, 2003, pp. 16–36.
[8] F. Képès, A. Rambourg, B. Satiat-Jeunemaitre, Morphodynamics of the secretory pathway, Int. Rev. Cytol. 242 (2005) 55–120.
[9] F. Brandizzi, S.L. Irons, J. Johansen, A. Kotzer, U. Neumann, GFP is the way to glow: bioimaging of the plant endomembrane system, J. Microsc. 214 (2004) 138–158.
[10] H.H. Mollenhauer, D.J. Morré, The Golgi apparatus, in: P. Stumpf, E. Conn (Eds.), The Biochemistry of Plants, Academic Press, New York, 1980, pp. 437–488.
[11] H.H. Mollenhauer, D.J. Morré, Structure of Golgi apparatus, Protoplasma 180 (1994) 14–28.
[12] B. Satiat-Jeunemaitre, C. Hawes, Redistribution of a Golgi glycoprotein in plant cells treated wit Brefeldin A, J. Cell Sci. 103 (1992) 1153–1166.
[13] P. Boevink, K. Oparka, S. Santa-Cruz, B. Martin, A. Betteridge, C. Hawes, Stacks on tracks: the plant Golgi apparatus traffics on an actin/ER network, Plant J. 15 (1998) 39.
[14] A. Nebenführ, L.A. Gallagher, T.G. Dunahay, J.A. Frohlick, A.M. Mazurkiewicz, J.B. Meehl, L.A. Staehelin, Stop- and-go movements of plant Golgi stacks are mediated by the acto-myosin system, Plant Physiol. 121 (1999) 1127–1141.
[15] A. Nebenführ, L.A. Staehelin, Mobile factories: Golgi dynamics in plant cells, Trends Plant Sci. 6 (2001) 160–167.
[16] F. Brandizzi, M. Fricker, C. Hawes, A greener world: the revolution in plant bioimaging, Nat. Rev., Mol. Cell Biol. 3 (2002) 520–530.
[17] T.H. Ward, F. Brandizzi, Dynamics of proteins in Golgi membranes: comparisons between mammalian and plant cells highlighted by photobleaching techniques, Cell Mol. Life Sci. 61 (2004) 172–185.
[18] F. Brandizzi, E.L. Snapp, A.G. Roberts, J. Lippincott-Schwartz, C. Hawes, Membrane protein transport between the endoplasmic reticulum and the Golgi in tobacco leaves is energy dependent but cytoskeleton independent: evidence from selective photobleaching, Plant Cell 14 (2002) 1293–1309.
[19] C.M. Saint-Jore, J. Evins, H. Batoko, F. Brandizzi, I. Moore, C. Hawes, Redistribution of membrane proteins between the Golgi apparatus and endoplasmic reticulum in plants is reversible and not dependent on cytoskeletal networks, Plant J. 29 (2002) 661–678.
[20] L.L.P. daSilva, E.L. Snapp, J. Denecke, J. Lippincott-Schwartz, C. Hawes, F. Brandizzi, ER export sites and Golgi bodies behave as single mobile secretory units in plant cells, Plant Cell 16 (2004) 1753–1771.
[21] G. Galili, ER-derived compartments are formed by highly regulated processes and have special functions in plants, Plant Physiol. 136 (2004) 3411–3413.
[22] I. Hara-Nishimura, R. Matsushima, T. Shimada, M. Nishimura, Diversity and formation of endoplasmic reticulum-derived compartments in plants. Are these compartments specific to plant cells? Plant Physiol. 136 (2004) 3435–3439.
[23] A. Vitale, A. Ceriotti, Protein quality control mechanisms and protein storage in the endoplasmic reticulum. A conflict of interests? Plant Physiol. 136 (2004) 3420–3426.
[24] I. Hara-Nishimura, T. Shiada, K. Hatano, Y. Takeuchi, M. Nishimura, Transport of storage proteins to protein storage vacuoles is mediated by large precursor-accumulating vesicles, Plant Cell 10 (1998) 825–836.
[25] N.C. Carpita, M. McCann, The cell wall, in: B.B. Buchanan, W. Gruissem, R.L. Jones (Eds.), Biochemistry and Molecular Biology of Plants, American Society of Plant Physiology, Rockville MD, USA, 2000, pp. 52–108.
[26] W.-R. Scheible, M. Pauly, Glycosyltransferases and cell wall biosynthesis: novel players and insights, Curr. Opin. Plant Biol. 7 (2004) 285–295.
[27] M. Pauly, P. Albersheim, A. Darvill, W.S. York, Molecular domains of the cellulose/xyloglucan network in the cell walls of higher plants, Plant J. 20 (1999) 629–639.
[28] S.C. Fry, Primary cell wall metabolism: tracking the careers of wall polymers in living plant cells, New Phytol. 161 (2004) 641–675.
[29] A.C. Fitchette-Lainé, V. Gomord, A. Chekkafi, L. Faye, Localization of xylosylation ad fucosylation in the plant Golgi apparatus, Plant J. 5 (1994) 673–682.
[30] C. Hawes, L. Faye, B. Satiat-Jeunemaitre, The Golgi apparatus and pathways of vesicle trafficking, in: M. Smallwood, P. Knox, D. Bowles (Eds.), Membranes: Specialized Functions in Plants, Bios Scientific Publishers, Oxford, 1996, pp. 337–365.
[31] K. Keegstra, N. Raikhel, Plant glycosyltransferases, Curr. Opin. Plant Biol. 4 (2001) 219–224.
[32] D. Dirnberger, P. Bencur, L. Mach, H. Steinkellner, The Golgi localization of *Arabidopsis thaliana* beta 1,2-xylosyltransferase in plant cells is dependent on its cytoplasmic and transmembrane sequences, Plant Mol. Biol. 50 (2002) 273–281.
[33] M.G. Handford, F. Sicilia, F. Brandizzi, J.H. Chung, P. Dupree, *Arabidopsis thaliana* expresses multiple Golgi-localised nucleotide-sugar transporters related to GONST1, Mol. Genet. Genomics 272 (2004) 397–410.
[34] P. Moreau, J.J. Bessoule, S. Mongrand, E. Testet, P. Vincent, C. Cassagne, Lipid trafficking in plant cells, Prog. Lipid Res. 37 (1998) 371–391.
[35] P. Mérigout, F. Képès, A.-M. Perret, B. Satiat-Jeunemaitre, P. Moreau, Effects of brefeldin A and nordihydroguaiaretic acid on

endomembrane dynamics and lipid synthesis in plant cells, FEBS Lett. 518 (2002) 88–92.
[36] J.-J. Bessoule, P. Moreau, Phospholipid synthesis and dynamics in plant cells, Top. Curr. Genet. 6 (2003) 89–124.
[37] F. Marty, Vacuoles, Plant Cell 11 (1999) 587–599.
[38] L.W. Jiang, J.C. Rogers, Sorting of lytic enzymes in the plant Golgi apparatus, in: D.G. Robinson (Ed.), The Golgi Apparatus and the Plant Secretory Pathway, Blackwell, Oxford, UK, 2003, pp. 114–140.
[39] L.C. Fowke, M.A. Tanchak, M.E. Galway, Ultrastructural cytology of the endocytotic pathway in plants, in: C.R. Hawes, J.O.D. Coleman, D.E. Evans (Eds.), Endocytosis, Exocytosis and Vesicle Traffic in Plants, Society for Experimental Biology Seminar Series, vol. 45, Cambridge Univ. Press, Cambridge, 1991, pp. 15–40.
[40] S. Bolte, C. Talbot, Y. Boutte, O. Catrice, N.D. Read, B. Satiat-Jeunemaitre, FM-dyes as experimental probes for dissecting vesicle trafficking in living plant cells, J. Microsc. 214 (2004) 159–173.
[41] N. Geldner, The plant endosomal system-ist structure and role in signal transduction and plant development, Planta 219 (2004) 547–560.
[42] J.E. Rothman, Mechanisms of intracellular protein transport, Nature 372 (1994) 55–63.
[43] D.G. Robinson, G. Hinz, S.E.H. Holstein, The molecular characterization of transport vesicles, Plant Mol. Biol. 38 (1998) 49–76.
[44] H.H. Mollenhauer, D.J. Morré, Tubular connections between dictyosomes and forming secretory vesicles in plant Golgi apparatus, J. Cell Biol. 29 (1966) 373–376.
[45] D.J. Morré, H.H. Mollenhauer, C.E. Bracker, Origin and continuity of Golgi apparatus, in: J. Reinsert, H. Upsprung (Eds.), Origin and Continuity of Cell Organelles, Springer Verlag, New York, 1971, pp. 98–117.
[46] D.J. Morré, J. Kartenbeck, W.W. Franke, Membrane flow and interconversions among endomembranes, Biochim. Biophys. Acta 559 (1979) 71–152.
[47] R.M. Brown, H. Kleining, H. Falk, P. Sitte, W. Franke, Scale formation in *Chrysophycean algae*, J. Cell Biol. 45 (1970) 246–271.
[48] G.I. MacFadden, M. Melkonian, Golgi apparatus activity and membrane flow during scale biogenesis in the green flagellate *Scherffelia dubia* (prasinophyceae) I. Flagellar regeneration, Protoplasma 130 (1986) 186–198.
[49] M. Melkonian, B. Becker, D. Becker, Scale formation in algae, J. Electron Microsc. Tech. 17 (1991) 165–178.
[50] D.S. Domozych, B. Wells, P.J. Shaw, Scale biogenesis in the green alga, *Mesostigma viride*, Protoplasma 167 (1992) 19–32.
[51] B. Becker, B. Bölinger, M. Melkonian, Anterograde transport of algal scales through the Golgi complex is not mediated by vesicles, Trends Cell Biol. 5 (1995) 305–307.
[52] B. Satiat-Jeunemaitre, C. Hawes, The distribution of secretory products in plant cells is affected by Brefeldin A, Cell Biol. Int. 17 (1993) 183–193.
[53] A. Driouich, G.F. Zhang, A.L. Staehelin, Effect of brefeldin A on the structure of the Golgi apparatus and on the synthesis and secretion of proteins and polysaccharides in sycamore maple (*Acer pseudoplatanus*) suspension-cultured cells, Plant Physiol. 101 (1993) 1363–1373.
[54] C. Ritzenthaler, A. Nebenführ, A. Movafeghi, C. Stussi-Garaud, L. Behnia, P. Pimpl, L.A. Staehelin, D.G. Robinson, Reevaluation of the effects of Brefeldin A on plant cells using tobacco Bright Yellow 2 cells expressing Golgi-targeted green fluorescent protein and COPI antisera, Plant Cell 14 (2002) 237–261.
[55] A.A. Sanderfoot, N.V. Raikhel, The specificity of vesicle trafficking: coat proteins and SNAREs, Plant Cell 11 (1999) 629–641.
[56] A. Nebenführ, Vesicle traffic in the endomembrane system: a tale of COPs, Rabs and SNAREs, Curr. Opin. Plant Biol. 5 (2002) 507–512.
[57] I. Contreras, E. Ortiz-Zapater, L.M. Castilho, F. Aniento, Characterization of COPI coat proteins in plant cells, Biochem. Biophys. Res. Commun. 273 (2000) 176–182.
[58] P. Pimpl, A. Movafeghi, S. Coughlan, J. Denecke, S. Hillmer, D.G. Robinson, In situ localization and in vitro induction of plant COPI-coated vesicles, Plant Cell 12 (2000) 2219–2235.
[59] B.A. Phillipson, P. Pimpl, L. Lamberti Pinto daSilva, A.J. Crofts, J.P. Tayler, A. Movafeghi, D.G. Robinson, J. Denecke, Secretory bulk flow of soluble proteins is efficient and COPII dependent, Plant Cell 13 (2001) 2005–2020.
[60] F. Aniento, B. Helms, A.R. Memon, How to make a vesicle: coat protein–membrane interactions, in: D.G. Robinson (Ed.), The Golgi Apparatus and the Plant Secretory Pathway, Blackwell, Oxford, UK, 2003, pp. 36–62.
[61] S. Bolte, S. Brown, B. Satiat-Jeunemaitre, The N-myristoylated Rab-GTPase m-Rabmc is involved in post-Golgi trafficking events to the lytic vacuole in plant cells, J. Cell Sci. 117 (2004) 943–954.
[62] S. Rutherford, I. Moore, The *Arabidopsis* Rab GTPase family: another enigma variation, Curr. Opin. Plant Biol. 5 (2002) 518–528.
[63] S. Rutherford, I. Moore, Rab proteins and the Golgi apparatus, in: D.G. Robinson (Ed.), The Golgi Apparatus and The Plant Secretory Pathway, Blackwell, Oxford, UK, 2003, pp. 165–180.
[64] A.A. Sanderfoot, F.F. Assaad, N.V. Raikhel, The *Arabidopsis* genome. An abundance of soluble N-ethylmaleimide-sensitive factor adaptor protein receptors, Plant Physiol. 124 (2000) 1558–1569.
[65] M.R. Blatt, G. Thiel, SNARE components and mechanisms of exocytosis in plants, in: D.G. Robinson (Ed.), The Golgi Apparatus and the Plant Secretory Pathway, Blackwell, Oxford, UK, 2003, pp. 208–237.
[66] P.R. Gilson, C.E. Vergara, L. Kjer-Nielson, R.D. Teasdale, A. Bacic, P.A. Gleeson, Identification of a Golgi-localised GRIP domain protein from *Arabidopsis thaliana*, Planta 219 (2004) 1050–1056.
[67] M.W. Steer, D. O'Driscoll, Vesicle dynamics and membrane turnover in plant cells, in: C. Hawes, J. Coleman, D. Evans (Eds.), Endocytosis, Exocytosis and Vesicle Traffic in Plants, Cambridge Univ. Press, Cambridge, 1991, pp. 129–142.
[68] J.M. Picton, M.W. Steer, The effect of cycloheximide on dictyosome activity in Tradescantia pollen tubes determined using cytochalasin D, Eur. J. Cell Biol. 29 (1983) 133–138.
[69] C. Hawes, C. Saint Jore, F. Brandizzi, Endomembrane and cytoskeleton interrelationships in higher plants, in: D. Robinson (Ed.), The Golgi Apparatus and the Plant Secretory Pathway, Blackwell, Oxford, UK, 2003, pp. 63–75.
[70] A.Y. Cheung, C.Y.-H. Chen, L.-z. Tao, T. Andreyeva, D. Twell, H.-m. Wu, Regulation of pollen tube growth by Rac-like GTPases, J. Exp. Bot. 54 (2003) 73–81.
[71] H. Quader, Formation and disintegration of cisternae of the endoplasmic reticulum visualized in live cells by conventional fluorescence and confocal laser scanning microscopy: evidence for involvement of calcium and the cytoskeleton, Protoplasma 155 (1990) 166–175.
[72] M. Fricker, A. Parsons, M. Tlalka, E. Blancaflor, S. Gilroy, A. Meyer, C. Plieth, Fluorescent probes for living plant cells, in: C. Hawes, B. Satiat-Jeunemaitre (Eds.), Plant Cell Biology A Practical Approach, Oxford Univ. Press, 2001, pp. 35–84.
[73] C. Kluge, T. Seidel, S. Bolte, S. Sharma, M. Hanitzsch, B. Satiat-Jeunemaitre, J. Rothmann, D. Golldack, K.-J. Dietz, Subcellular distribution of the V-ATPase complex in plant cells, and in vivo localisation of the 100 kDa subunit VHA-a within the complex, BMC 5 (2004) 29.
[74] R.M. Napier, L.C. Fowke, C. Hawes, M. Lewis, H. Pelham, Immunological evidence that plants use both HDEL and KDEL for targeting proteins to the endoplasmic reticulum, J. Cell Sci. 102 (1992) 261–271.
[75] A.C. Fitchette, M. Cabanes-Macheteau, L. Marvin, B. Martin, B. Satiat-Jeunemaitre, V. Gomord, K. Crooks, P. Lerouge, L. Faye, C. Hawes, Biosynthesis and immunolocalization of Lewis a-containing N-glycans in the plant cell, Plant Physiol. 121 (1999) 333–344.

[76] D. Essl, D. Dirnberger, V. Gomord, R. Strasser, L. Faye, J. Glössl, H. Steinkellner, The N-terminal 77 amino acids from tobacco N-acetylglucosoaminyltransferase I are sufficient to retain a reporter protein in the Golgi apparatus of *Nicotiana benthamiana* cells, FEBS Lett. 453 (1999) 169–173.
[77] T.C. Baldwin, M.G. Handford, M.I. Yuseff, A. Oorellana, P. Dupree, Identification and characterization of GONST1, a Golgi-localized GDP-mannose transporter in *Arabidopsis*, Plant Cell 13 (2001) 2283–2295.
[78] S. Munro, Localization of proteins to the Golgi apparatus, Trends Cell Biol. 8 (1998) 11–15.
[79] E.G.-T. Wee, D.J. Sherrier, T.A. Prime, P. Dupree, Targeting of active sialyl transferase to the plant Golgi apparatus, Plant Cell 10 (1998) 1759–1768.
[80] B. Satiat-Jeunemaitre, C. Steele, C. Hawes, Golgi-membrane dynamics are cytoskeleton dependent: a study on Golgi stack movement induced by brefeldin A, Protoplasma 191 (1996) 21–33.
[81] L. Liu, Y.R. Lee, R. Pan, J.N. Maloof, B. Liu, An internal motor kinesin is associated with the Golgi apparatus and plays a role in trichome morphogenesis in *Arabidopsis*, Mol. Biol. Cell 16 (2005) 811–823.
[82] M.L. Preuss, D.R. Kovar, Y.-R. Lee, C.T.J. Staiger, D.P. Delmer, B. Liu, A plant-specific kinesin binds to actin microfilaments and interacts with cortical microtubules in cotton fibers, Plant Physiol. 136 (2004) 3945–3955.
[83] A.V. Andreeva, H. Zheng, C.M. Saint-Jore, M.A. Kutuzov, D.E. Evans, C.R. Hawes, Organization of transport from endoplasmic reticulum to Golgi in higher plants, Biochem. Soc. Transact. 28 (2000) 505–512.
[84] M. Bar-Peled, N. Raikhel, Characterization of AtSEC12 and AtSAR1. Proteins likely involved in endoplasmic reticulum and Golgi transport, Plant Physiol. 114 (1997) 315–324.
[85] C. D'Enfert, M. Geusse, C. Gaillardin, Fission yeast and a plant have functional homologues of the Sar1 and Sec12 proteins involved in ER to Golgi traffic in budding yeast, EMBO J. 11 (1992) 4205–4210.
[86] A. Movafeghi, N. Happel, P. Pimpl, G.H. Tai, D.G. Robinson, *Arabidopsis* Sec21p and Sec23p homologs. Probable coat proteins of plant COP-coated vesicles, Plant Physiol. 119 (1999) 1437–1445.
[87] M. Takeuchi, T. Ueda, K. Sato, H. Abe, T. Nagata, A. Nakano, A dominant negative mutant of Sar1 GTPase inhibits protein transport from the endoplasmic reticulum to the Golgi apparatus in tobacco and *Arabidopsis* suspension cultured cells, Plant J. 23 (2000) 517–525.
[88] C.G. Giraudo, J.F. Maccioni, Endoplasmic reticulum export of glycosyl transferases depends on interaction of a cytoplasmic dibasic motif with Sar1, Mol. Biol. Cell 14 (2003) 3753–3766.
[89] O.W. Rossanese, J.S. Soderholm, B.J. Bevis, I.B. Sears, J. O'Connor, E.K. Williamsn, B.S. Glick, Golgi structure correlates with transitional endoplasmic reticulum organisation in *Pichia pastoris* and *Saccharomyces cerevisia*, J. Cell Biol. 145 (1999) 69–81.
[90] C. Barlowe, COPII-dependent transport from the endoplasmic reticulum, Curr. Opin. Cell Biol. 14 (2002) 417–422.
[91] K. Törmäkanagas, J.L. Hadlington, P. Pimpl, S. Hillmer, F. Brandizzi, T.H. Teeri, J. Denecke, A vacuolar sorting domain may also influence the way in which proteins leave the endoplasmic reticulum, Plant Cell 13 (2001) 2021–2032.
[92] K.J. Palmer, D.J. Stephens, Biogenesis of ER-to-Golgi transport carriers: complex roles of COPII in ER export, Trends Cell Biol. 14 (2004) 57–61.
[93] A.A. Mironov, G.V. Mironov Jr., A. Beznoussenko, P. Trucco, J.D. Lupetti, W.J.C. Smith, A.J. Geets, K.N.J. Koster, M.E. Burger, T.J. Martone, M.H. Deernick, A. Ellisman, Luini, ER-to-Golgi carriers arise through direct en bloc protrusion and multistage maturation of specialized ER exit domains, Dev. Cell 5 (2003) 1–20.
[94] I. Contreras, E. Ortiz-Zapater, F. Aniento, Sorting signals in the cytosolic tail of membrane proteins involved in the interaction with plant ARF1 and coatomer, Plant J. 38 (2004) 685–698.
[95] I. Couchy, S. Bolte, M.-T. Crosnier, S. Brown, B. Satiat-Jeunemaitre, Identification and localization of a-COP-like protein involved in the morphodynamics of the plant Golgi apparatus, J. Exp. Bot. 54 (2003) 2053–2063.
[96] N. Geldner, N. Anders, H. Wolters, J. Keicher, W. Komberge, P. Muller, A. Delbarre, T. Ueda, A. Nakano, G. Jürgens, The *Arabidopsis* GNOM ARF-GEF mediates endosomal recycling, auxin transport and auxin-dependent plant growth, Cell 112 (2003) 219–230.
[97] M. Takeuchi, T. Ueda, N. Yahara, A. Nakano, Arf1 GTPase plays roles in the protein traffic between the ER and the Golgi apparatus in tobacco and *Arabidopsis* cultured cells, Plant J. 31 (2002) 499–515.
[98] M.H. Lee, M.K. Min, Y.J. Lee, J.B. Jin, D.H. Shin, D.H. Kim, K.-H. Lee, I. Hwang, ADP-ribosylation factor 1 of arabidopsis plays a critical role in intracellular trafficking and maintenance of endoplasmic reticulu morphology in *Arabidopsis*, Plant Physiol. 129 (2002) 1507–1520.
[99] N. Yahara, A. Nakano, Arf1 GTPase plays roles in the protein traffic between the endoplasmic reticulum and the Golgi apparatus in tobacco and *Arabidopsis* cultured cells, Plant J. 31 (2002) 499–515.
[100] P. Pimpl, S. Hanton, J.P. Taylor, L.L. Pinto-daSilva, J. Denecke, The GTPase ARF1p controls the sequence-specific vacuolar sorting route to the lytic vacuole, Plant Cell 15 (2003) 1242–1256.
[101] G. Jürgens, N. Geldner, Protein secretion in plants: from the trans-Golgi network to the outer space, Traffic 3 (2002) 605–613.
[102] V. Vernoud, A.C. Horton, Z. Yang, E. Nielsen, Analysis of the small GTPase gene superfamily of *Arabidopsis*, Plant Physiol. 131 (2003) 1191–1208.
[103] N.R. Altan-Bonnet, R. Sougrat, J. Lippincott-Schwartz, Molecular basis for Golgi maintenance and biogenesis, Curr. Opin. Cell Biol. 16 (2004) 364–372.
[104] T. Uemera, T. Ueda, R.L. Ohniwa, A. Nakano, K. Takeyasu, M.H. Sato, Systematic analyses of SNARE molecules in *Arabidopsis*: dissection of the post-Golgi network in plant cells, Cell Struct. Funct. 29 (2004) 49–65.
[105] H. Batoko, H.Q. Zheng, C. Hawes, I. Moore, A Rab1 GTPase is required for transport between the endoplasmic reticulum and Golgi apparatus and for normal Golgi movement in plants, Plant Cell 12 (2000) 2201–2217.
[106] A.Y. Cheung, C.Y.-H. Chen, R.H. Glaven, B.H.J. de Graaff, L. Vidali, P.K. Hepler, H.-M. Wu, Rab2 GTPase regulates trafficking between the endoplasmic reticulum and the Golgi bodies and is important for pollen tube growth, Plant Cell 14 (2002) 945–962.
[107] P.K. Hepler, B.A. Palevitz, S.A. Lancelle, M. McCauley, I. Lichtscheidl, Cortical endoplasmic reticulum in plants, J. Cell Sci. 96 (1990) 355–373.
[108] I.K. Lichtscheidl, P.K. Hepler, Endoplasmic reticulum in the cortex of plant cells, in: M. Smallwood, J.P. Knox, D.J. Bowles (Eds.), Membranes Specialised Functions in Plants, Bios Scientific Publishers, 1996, pp. 383–402.
[109] B. Juniper, C.R. Hawes, J.C. Horne, The relationship between dictyosomes and the forms of endoplasmic reticulum in plant cells with different export programs, Bot. Gaz. 143 (1982) 135–145.
[110] N. Harris, K.J. Oparka, Connections between dictyosomes, ER and GERL in cotyledons of mung bean (*Vigna radiata* L.), Protoplasma 114 (1983) 93–102.
[111] H.H. Mollenhauer, W.G. Whaley, An observation on the functioning of the Golgi apparatus, J. Cell Biol. 17 (1963) 222–225.
[112] G. Hinz, E. Herman, Sorting of storage proteins in the plant Golgi apparatus, in: D.G. Robinson (Ed.), The Golgi Apparatus and the Plant Secretory Pathway, Blackwell, Oxford, UK, 2003, pp. 141–164.
[113] B. Wenzel, G. Schauerman, A. von Lüpke, G. Hinz, The cargo in vacuolar storage protein transport vesicles is stratified, Traffic 6 (2005) 1–11.
[114] W.P. Cunningham, D.J. Morré, H.H. Mollenhauer, Structure of

isolated plant Golgi apparatus revealed by negative staining, J. Cell Biol. 28 (1966) 169–179.
[115] M.L. Parker, C. Hawes, The Golgi apparatus in developing endosperm of wheat *triticum sativum* L., Planta 154 (1982) 277–283.
[116] L.A. Staehelin, T.H. Giddings Jr., J.Z. Kiss, F.D. Sack, Macromolecular differentiation of Golgi stacks in root tips of *Arabidopsis* and *Nicotiana* seedlings as visualized in high pressure frozen and freeze-substituted samples, Protoplasma 157 (1990) 75–91.
[117] Y.C. Tse, B. Mo, S. Hillmer, M. Zhao, S.W. Lo, D.G. Robinson, L. Jiang, Identification of multivesicular bodies as prevacuolar compartments in *Nicotiana tabacum* BY-2 cells, Plant Cell 16 (2004) 672–693.
[118] A.A. Sanderfoot, S.U. Ahmed, D. Marty-Mazars, I. Rapoport, T. Kirchhausen, F. Marty, N.V. Raikhel, A putative vacuolar cargo receptor partially colocalizes with AtPEP12p on a prevacuolar compartment in *Arabidopsis* roots, Proc. Natl. Acad. Sci. U. S. A. 95 (1998) 9920–9925.
[119] A.A. Sanderfoot, V. Kovaleva, D.C. Bassham, N.V. Raikhel, Interactions between syntaxins identify at least five SNARE complexes within the Golgi/prevacuolar system of the *Arabidopsis* cell, Mol. Biol. Cell 12 (2001) 3733–3743.
[120] A.M. Kotzer, F. Brandizzi, U. Neumann, N. Paris, I. Moore, C. Hawes, AtRabF2b (Ara7) acts on the vacuolar trafficking pathway in tobacco leaf epidermal cells, J. Cell Sci. 117 (2004) 6377–6389.
[121] B. Satiat-Jeunemaitre, L. Cole, T. Bourett, R. Howard, C.R. Hawes, Brefeldin A effects in plant and fungal cells: something new about vesicle trafficking? J. Microsc. 181 (1996) 162–177.
[122] B. Lefebvre, H. Batoko, G. Duby, M. Boutry, Targeting of a Nicotiana plumbaginifolia H+-ATPase to the plasma membrane is not by default and requires cytosolic structural determinants, Plant Cell 16 (2004) 1772–1789.
[123] P. Boevink, B. Martin, K.J. Oparka, S. Santa Cruz, C. Hawes, Transport of virally expressed green fluorescent protein through the secretory pathway in tobacco leaves is inhibited by cold shock and Brefeldin A, Planta 208 (1999) 392–400.
[124] B. Vian, Ultrastructural localisation of carbohydrates, in: J. Bailey (Ed.), Recent Developments in Cytochemistry and Affinity Methods, NATO ASI Series, vol. H1, Springer Verlag, Berlin Heidelberg, 1986, pp. 49–57.
[125] D.J. Sherrier, K.A. Vanden Bosch, Secretion of cell wall polysaccharides in *Vicia* root hairs, Plant J. 5 (1990) 185–195.
[126] L.A. Staehelin, T.H. Giddings, S. Levy, M.A Lynch, P.J. Moore, K.M.M. Swords, Organisation of the secretory pathway of cell wall glycoproteins and complex poilysaccharides in plant cells, in: C. Hawes, J. Coleman, D. Evans (Eds.), Endocytosis, Exocytosis and Vesicle Traffic In Plants, Cambridge Univ. Press, 1991, pp. 183–198.
[127] J.L. Hadlington, J. Denecke, Sorting of soluble proteins in the secretory pathway of plants, Curr. Opin. Plant Biol. 3 (2000) 461–468.
[128] H. Hofte, M.J. Chrispeels, Protein sorting to the vacuolar membrane, Plant Cell 4 (1992) 995–1004.
[129] A. Vitale, N. Raikhel, What do proteins need to reach different vacuoles? Trends Plant Sci. 4 (1999) 149–155.
[130] F. Brandizzi, N. Frangne, S. Marc-Martin, C. Hawes, J.M. Neuhaus, N. Paris N, The destination for single-pass membrane proteins is influenced markedly by the length of the hydrophobic domain, Plant Cell 14 (2002) 1077–1092.
[131] B. Leymann, D. Geelen, F.J. Quintero, M.R. Blatt, A tobaco syntaxin with a role in hormonal control of guard cell ion channels, Science 283 (1999) 537–540.
[132] N. Geldner, J. Friml, Y.D. Stierhof, G. Jürgens, K. Palme, Auxin transport inhibitors block PIN1 cycling and vesicle trafficking, Nature 413 (2001) 425–428.
[133] W. Lukowitz, U. Mayer, G. Jurgens, Cytokinesis in the *Arabidopsis* embryo involves the syntaxin-related KNOLLE gene products, Cell 84 (1996) 61–71.
[134] S.Y. Bednarek, T.G. Falbel, Membrane trafficking during plant cytokinesis, Traffic 3 (2002) 621–629.
[135] G. Jürgens, T. Pacher, Cytokinesis: membrane trafficking by default? Annu. Plant Rev. 9 (2003) 238–254.
[136] I. Muller, W. Wagner, A. Volke, S. Schellmann, P. Nacry, F. Kuttner, Z. Schwarz-Sommer, U. Mayer, G. Jurgens, Syntaxin specificity of cytokinesis in *Arabidopsis*, Nat. Cell Biol. 5 (2003) 531–534.
[137] D.N. De, Plant Cell Vacuoles, CSIRO publishing, Collinwood, Australia, 2000.
[138] L.W. Jiang, J.C. Rogers, Integral membrane protein sorting to vacuoles in plant cells: evidence for two pathways, J. Cell Biol. 143 (1998) 1183–1199.
[139] S. Hillmer, A. Movafeghi, D.G. Robinson, G. Hinz, Vacuolar storage proteins are sorted in the cis-cisternae of the pea cotyledon Golgi apparatus, J. Cell Biol. 152 (2001) 41–50.
[140] L. Frigerio, M. de Virgilio, A. Prada, F. Faoro, A. Vitale, Sorting of phaseolin to the vacuole is saturable and requires a short C-terminal peptide, Plant Cell 10 (1998) 1031–1042.
[141] T. Kirsch, N. Paris, J.M.N. Butler, L. Beevers, J.C. Robers, Purification and initial characterization of a potential plant vacuolar targeting receptor, Proc. Natl. Acad. Sci. U. S. A. 91 (1994) 3403–3407.
[142] N. Paris, J.M. Neuhaus, BP-80 as a vacuolar sorting receptor, Plant Molec. Biol. 50 (2002) 903–914.
[143] S.U. Ahmed, E. Rokjo, S. Venkataraman, J.E. Dombrowski, K. Matsuoka, N.V. Raikhel, The plant vacuolar sorting receptor AtELP is involved in transport of NH2-terminal propeptide-containing vacuolar proteins in *Arabidopsis thaliana*, J. Cell Biol. 149 (2000) 1335–1344.
[144] G. Hinz, S. Hillmer, M. Baumer, I. Hohl, Vacuolar storage proteins and the putative vacuolar sorting receptor BP-80 exit the Golgi apparatus of developing pea cotyledons in different transport vesicles, Plant Cell 11 (1999) 1509–1524.
[145] N. Mitsuhashi, T. Shimada, S. Mano, M. Nishimura, I. Hara-Nishimura, Characterization of organelles in the vacuolar-sorting pathway by visualization with GFP in tobacco BY-2 cells, Plant Cell Physiol. 41 (2000) 993–1001.
[146] N. Mitsuhashi, Y. Hayashi, Y. Koumoto, T. Shimada, T. Fukasawa-Akada, M. Nishimura, I. Hara-Nishimura, A novel membrane protein that is transported to protein storage vacuoles via precursor-accumulating vesicles, Plant Cell 13 (2001) 2361–2372.
[147] A. Da Silva Conceicao, D. Maety-Mazars, D.C. Bassham, A.A. Sanderfoot, F. Marty, N.V. Raikhel, The syntaxin homolog At-PEP12p resides on a late post-Golgi compartment in plants, Plant Cell 9 (1997) 571–582.
[148] D.C. Bassham, A.A. Sanderfoot, V. Kovaleva, H. Zheng, N.V. Raikhel, AtVPS45 complex formation at the trans-Golgi network, Mol. Biol. Cell 11 (2000) 2251–2265.
[149] Y.B. Li, S.W. Rogers, Y.C. Tse, S.W. Lo, S.S.M. Sun, G.Y. Jauh, L.W. Jiang, BP-80 homologs are concentrated on post-Golgi, probably lytic prevacuolar compartments, Plant Cell Physiol. 43 (2002) 726–742.
[150] M.A. Tanchak, L.C. Fowke, The morphology of multivesicular bodies in soybean protoplasts and their role in endocytosis, Protoplasma 138 (1987) 173–182.
[151] M.A. Tanchak, L.R. Griffing, B.G. Mersey, L.C. Fowke, Endocytosis of cationized ferritin by coated vesicles of soybean protoplasts, Planta 162 (1984) 481–486.
[152] N.A. Jolliffe, J.C. Brown, U. Neumann, M. Vicré, C. Hawes, A. Ceriotti, L.M. Roberts, L. Frigerio, Transport of ricin and 2S albumin precursors to the storage vacuoles of *Ricinus comunis* endosperm involves the Golgi and VSR-like receptors, Plant J. 39 (2004) 821–833.
[153] T. Shimada, K. Fuji, K. Tamura, M. Kondo, M. Nishimura, I. Hara-Nishimura, 2003. Vacuolar sorting receptor for seed storage proteins in *Arabidopsis thaliana*, Proc. Natl. Acad. Sci. 100 (2003) 16095–16100.

[154] B.J. Jin, Y.A. Ki, S.J. Kim, S.H. Less, D.H. Kim, G.-W. Cheong, I. Hwang, A new dynamin-like protein, ADL6, is involved in trafficking from the trans-Golgi network to the central vacuole in *Arabidopsis*, Plant Cell 13 (2001) 1511–1525.
[155] L.A. Staehelin, I. Moore, The plant Golgi apparatus: structure, functional organization and trafficking mechanisms, Annu. Rev. Plant Physiol. Plant Mol. Biol. 46 (1995) 261–288.
[156] T.C. Pesacreta, W.J. Lucas, Presence of a partially-coated reticulum in angiosperms, Protoplasma 125 (1985) 173–184.
[157] S. Hillmer, H. Freundt, D.G. Robinson, The partially coated reticulum and its relationship to the Golgi apparatus in higher plants, Eur. J. Cell Biol. 47 (1988) 206–212.
[158] B.J. Bevis, A.T. Hammond, C.A. Reinke, B.S. Glick, De novo formation of transitional ER sites and Golgi structures in *Pichia pastoris*, Nat. Cell Biol. 4 (2002) 750–756.
[159] K.J.M. Zaal, C.L. Smith, R.S. Polishchuk, N. Altan, N.B. Cole, J. Ellenberg, K. Hirschberg, J.F. Presley, T.H. Roberts, E. Siggia, R.D. Phair, J. Lippincott-Schwartz, Golgi membranes are absorbed into and reemerge from the ER during mitosis, Cell 99 (1999) 589–601.
[160] F.R. Turner, W.G. Whaley, Intercisternal elements of the Golgi apparatus, Science 147 (1965) 1303–1304.
[161] C.L. de Graffenried, C.R. Bertozzi, The roles of enzyme localisation and complex formation in glycan assembly within the Golgi apparatus, Curr. Opin. Cell Biol. 16 (2004) 356–363.
[162] F.A. Barr, B. Short, Golgins in the structure and dynamics of the Golgi apparatus, Curr. Opin. Cell Biol. 15 (2003) 403–416.
[163] J. Klumperman, The growing Golgi: in search of its independence, Nat. Cell Biol. 2 (2000) E1–E2.
[164] J. Klumperman, Transport between ER and Golgi, Curr. Opin. Cell Biol. 12 (2000) 445–449.
[165] A. Murshid, J.F. Presley, ER- to -Golgi transport and cytoskeletal interactions in animal cells, Cell. Mol. Life Sci. 61 (2004) 133–145.
[166] A. Rose, M. Sankaraganesh, S.J. Schraegle, M.A. Maloy, E.A. Stahlberg, I. Meier, Genome-wide identification of *Arabidopsis* coiled-coil proteins and establishment of the ARABI-COIL database, Plant Physiol. 134 (2004) 927–939.
[167] R.S. Polishchuk, A.A. Mironov, Structural aspects of Golgi function, Cell Mol. Life Sci. 61 (2004) 146–158.